

# Gas Exchange and Water Relations in Diploid and Tetraploid Russian Wildrye

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## ABSTRACT

Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski] is a drought tolerant, cool-season forage grass used in seeded pastures in the Northern Great Plains where water often limits production. Seedling vigor is generally poor in diploid cultivars, but tetraploid germplasm has improved seedling vigor. Objectives of this study were to determine the relationships between water-use efficiency (WUE), carbon isotope discrimination (CID), and gas exchange rates for a diploid cultivar (Vinall) and a tetraploid entry over 3 yr, two water treatments (50 and 150% of mean monthly precipitation), and two fertilizer rates (10 and 134 kg N ha<sup>-1</sup>) in a rain shelter. The tetraploid entry exhibited higher carbon exchange rate (CER), stomatal conductance (gs), and transpiration (T) than the diploid entry at the 50% but not the 150% water treatment. Leaf water potentials (LWP) were 0.6 and 0.3 MPa less negative for the tetraploid entry than diploid entry at the 50 and 150% water treatment, respectively. Values of CER averaged 12.4 and 14.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , T averaged 5.2 and 6.0  $\text{mmol m}^{-2} \text{s}^{-1}$ , and gs averaged 0.21 and 0.28  $\text{mol m}^{-2} \text{s}^{-1}$  for the diploid and tetraploid entry, respectively. The diploid entry had a significantly greater CID, averaging 20.37‰ compared with 19.65‰ for the tetraploid entry and CID was negatively associated with WUE. The more favorable plant water relations, gas exchange, and dry matter production under limited soil water suggests tetraploid populations of Russian wildrye should be emphasized in future breeding and management programs.

Russian wildrye is a productive, cool-season bunchgrass that is used for seeding improved pastures in the semiarid Northern Great Plains of the USA and Canada (Rogler and Schaaf, 1963). It has high drought tolerance yet maintains high nutritive value for dormant grazing. Because water often limits forage production in this area, adequate seasonal precipitation and stored soil water are needed to sustain production of forage grasses (Rogler and Haas, 1947; Smika et al., 1965; Sneva, 1977).

Poor seedling vigor, often associated with stand establishment failures, has prevented more widespread use of Russian wildrye (Lawrence, 1963). Cultivar releases of diploid Russian wildrye with improved seedling vigor include Swift (Lawrence, 1979), Bozoiisky-Select (Asay et al., 1985), and Mankota (Berdahl et al., 1992). Natural and derived tetraploids of Russian wildrye have considerably better seedling vigor compared with diploid cultivars in both greenhouse (Lawrence et al., 1990; Berdahl and Barker, 1991; Jefferson, 1993; Asay et al., 1996) and field (Berdahl and Ries, 1997) studies.

Advances in understanding the relationship between WUE and CID (Farquhar and Richards, 1984) have

been encouraging for selecting forage grasses with improved WUE (the amount of dry matter produced per unit of water transpired) and dry matter production (Ehleringer et al., 1990; Johnson and Bassett, 1991; Johnson et al., 1990; Read et al., 1991; Read et al., 1993). Dry matter production can be either positively or negatively associated with CID (Farquhar and Richards, 1984). Read et al. (1993) found no correlation between CID and forage yield for nine clones of crested wheatgrass [*Agropyron desertorum* (Fischer ex Link) Schultes]. Johnson and Bassett (1991) reported a negative correlation between CID and WUE in tall fescue (*Festuca arundinacea* Schreb.), orchardgrass (*Dactylis glomerata* L.), perennial ryegrass (*Lolium perenne* L.), and crested wheatgrass grown in the greenhouse. Johnson et al. (1990) reported a negative correlation between CID and WUE for crested wheatgrass and Altai wildrye [*Leymus angustus* (Trin.) Pilger]. Read et al. (1991) showed a similar negative relationship for crested wheatgrass grown under both well watered and drought conditions. Ehleringer et al. (1990), however, reported a positive correlation between forage yield and CID in crested wheatgrass.

The objectives of this study were to determine the gas exchange properties and their relationship to WUE and CID in field-grown diploid and tetraploid entries of Russian wildrye grown at two N and two water levels. The levels of N and water treatments were selected to provide a range of growing conditions similar to managed pastures.

## MATERIALS AND METHODS

Diploid and tetraploid entries of Russian wildrye were seeded in plots consisting of eight rows (3.6-m length, 0.33-m row spacing) in a rain shelter (11 by 30 m) on 13 May 1992. The seeding rate was 90 seeds m<sup>-1</sup> row length, which is a typical seeding rate for Russian wildrye. The tetraploid entry consisted of a balanced composite of six populations and is representative of tetraploid germplasm in the breeding program at Mandan. The diploid entry was the cultivar Vinall (released in 1960), a standard of comparison in many studies with Russian wildrye. The rain shelter automatically covered the plot area during rainfall events from 1 April to 1 November each year. An overhead sprinkling system in the rain shelter was used to supply water for seedling establishment and impose water treatments after establishment. The soil was a Parshall fine sandy loam (coarse-loamy, mixed Pachic Haploborolls).

Four replicates of each entry were arranged in a split-plot design with repeated measures across years (1994, 1995, 1996). Main plots were water treatments providing 50 and 150% of the long-term mean monthly precipitation for the April

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**Abbreviations:** CER, carbon exchange rate; Ci/Ca, atmospheric carbon dioxide concentration/leaf intercellular carbon dioxide concentration; CID, carbon isotope discrimination; GDD, growing degree-days; gs, stomatal conductance; LWP, leaf water potential; T, transpiration; WUE, water-use efficiency.

through October period. The long-term (30 yr) average precipitation for April, May, June, July, August, September, and October at Mandan, ND, is 38, 55, 85, 61, 43, 38, and 24 mm, respectively. The appropriate quantity of water was applied equally on Wednesday and sometimes on Thursday of each week to achieve these monthly totals. The rain shelter was set to the open position from November through March each year allowing the Russian wildrye to be exposed to winter precipitation. Subplots were randomized within water treatments and included entries and N fertilizer rates ( $\text{NH}_4\text{NO}_3$ ) broadcast at 10 and 134 kg N  $\text{ha}^{-1}$  in April each year. The two water and N treatments were established in 1993, and measurements from various treatment plots were commenced in 1994.

Carbon exchange rate, gs, and T were measured with a portable photosynthesis unit (Model LCA-4, Analytical Development Co., Hoddesdon, England). Measurements were made on the leaf subtending the flag leaf, as the flag leaves were too small for cuvette measurements, on 11, 20, 25, and 31 May 1994; on 24, 31 May, and 5, 12 June 1995; and on 29 May, 5, 10, and 17 June 1996. Measurements were taken on clear or nearly clear days starting at about 1300 h except on days when water was applied. The cuvette conditions (air temperature, relative humidity, and  $\text{CO}_2$  concentration) were set to ambient, and the leaf was exposed to a mean photosynthetically active radiation level of  $1775 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Three leaves were measured separately for each treatment and replication. Leaf water potentials were measured at 1300 h with thermocouple psychrometers on the same position leaf and same dates as CER, gs, and T. Leaves were removed from the plant, immediately placed in the psychrometer, transported to the lab, and measured after vapor equilibrium in a constant temperature water bath at  $25^\circ\text{C}$ .

Carbon isotope discrimination was measured on the same position leaf used for CER determination. About 20 leaves were collected and composited from each treatment and replication on 23 June, 1994 (ripe seed stage) and on 14 June, 1995 (anthesis). Leaves were placed in paper bags, stored on ice, transported to the laboratory, and dried at  $70^\circ\text{C}$  for 48 h. The dried leaves were ground twice to pass through a 0.64-mm screen with a Wiley mill (Arthur H. Thomas Co., Philadelphia, PA). Analyses for CID determinations were made with a SIRA 10 isotope ratioing mass spectrometer (Fisons Instruments, Valencia, CA) by procedures previously described (Johnson et al., 1990). Results were expressed as the ratio of  $^{13}\text{C}/^{12}\text{C}$  relative to Pee Dee belemnite standard (PBD), and CID was calculated according to Farquhar et al. (1989) using a  $\delta^{13}\text{C}$  value of ambient air of  $-8.00$  per mil on the PBD scale.

Soil water content for calculating field WUE was measured with a neutron probe on 7 April 1994, 25 April 1995, 23 April 1996, and after each year's final harvest. The access tubes were placed between rows in the center of each plot. Soil water content was similar for all plots on 27 April 1993 averaging 281 and 282 mm for the diploid and tetraploid entry, respectively. Measurements were made with the probe placed at 0.3-m increments to 1.2-m depth. Total water used was determined from soil water loss as measured from neutron probe measurements and applied water during the interval from the first neutron measurement in April each year through final dry matter harvest.

Soil water potential was measured weekly using thermocouple psychrometers at the 45-cm depth to provide an indication of the soil water stress the plants were exposed to in each water treatment throughout the growing season. Soil water potentials were standardized to  $25^\circ\text{C}$ .

A small error in soil water content has been associated with neutron probe measurements from the soil surface to 0.15-m

depth because of possible neutron escape, especially in soils with textural discontinuities. Available soil water at  $-0.03$  MPa matric potential averaged 47 mm per 0.3-m increment in the Parshall soil, which has essentially uniform texture throughout the profile. Water was applied weekly, and both Russian wildrye entries established a canopy early in the season. As a result, we assumed that any errors resulting from escaping neutrons were negligible. Total evapotranspiration was calculated as the sum of soil water lost to 1.2-m depth between the two soil water measurements plus water applied by irrigation. Field-measured WUE, defined as the amount of dry matter produced per unit of water lost from the soil, was calculated from evapotranspiration and forage dry matter determined at the final harvest.

Plant development based on leaf exsertion was referenced to the Haun scale (Haun, 1973), and development through heading and seed formation stages was referenced to the Haun scale as modified by Bauer et al. (1989). Five plants per plot were scored three times weekly. Forage dry matter was determined at five growth stages prior to plant maturity by clipping a  $0.1\text{-m}^2$  area in 1994 and 1995 and  $0.15\text{-m}^2$  area in 1996 from each plot to a 2-cm stubble height. Dry weight of the clipped forage was determined after drying at  $70^\circ\text{C}$  to a constant weight. Final forage yields for calculating WUE were taken at seed dough stage (Haun stage 9.0) from a  $0.2\text{-m}^2$  area in 1994, 1995, and 1996.

Statistical analysis was conducted by SAS proc mixed with repeated measures (Littell et al., 1996). Mean differences were determined by orthogonal contrasts with single-degree-of-freedom comparisons. Statistical significance is reported at the 0.05 level of probability unless stated otherwise.

## RESULTS AND DISCUSSION

Both diploid and tetraploid Russian wildrye developed five leaves (Haun Stage 5) prior to the boot, stem extension, and heading stages of development. The latter stages corresponded to Haun stages 6 through 9 (Bauer et al., 1989). The rate of leaf exsertion on the stems was similar for both entries and was linearly related to accumulated growing degree-days (GDD) with the diploid and tetraploid entries requiring 87 and 88 GDD per leaf, respectively. Both entries developed early and rapidly, and heading (Haun Stage 9) was completed by 10 June of each year.

A significant entry  $\times$  water treatment  $\times$  Haun stage interaction was present for dry matter production (Fig. 1). Above-ground dry matter production was greater for the tetraploid than diploid entry at the last three Haun stages in the 50% water treatment. In the 150% water treatment, dry matter production was similar for both entries at all sampling stages. The significant interaction was due to the greater amount of dry matter produced at the final three Haun stages by the tetraploid compared with the diploid entry at deficit soil water conditions created by the 50% water treatment. The lower dry matter production by the tetraploid at the 150% compared with the 50% water treatment was due to lower dry matter production at the 10 kg N  $\text{ha}^{-1}$  fertilizer rate (data not shown). This decrease may have been caused by either the extra water (150%) leaching some N below the root zone or inadequate soil N (10 kg N  $\text{ha}^{-1}$  rate) to meet the needs of the tetraploid entry.

In the 150% water treatment, soil water potentials determined with thermocouple psychrometers at the 10

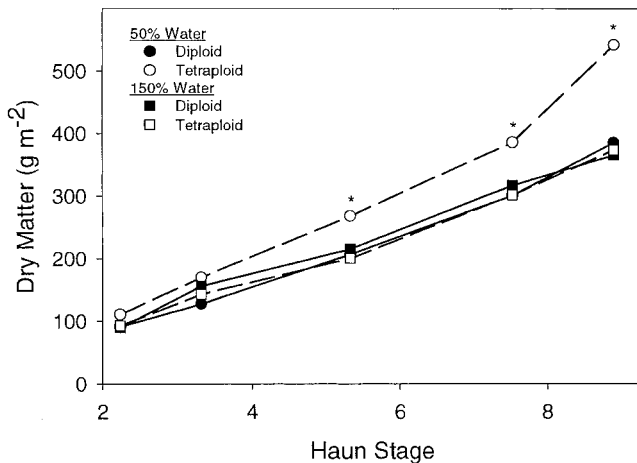


Fig. 1. Dry matter production for diploid and tetraploid entries of Russian wildrye grown at 50 and 150% of average rainfall. Data are means for 1994, 1995, and 1996. Significance at the 0.05 level of probability, as indicated with an \*, was present between the tetraploid and diploid entry at the 50% water treatment, but not between entries at the 150% water treatment.

and 134 kg N ha<sup>-1</sup> rates were similar for both the diploid and tetraploid entries (Fig. 2). In the 50% water treatment at the 10 and 134 kg N ha<sup>-1</sup> rate, the diploid entry extracted soil water to a lower soil water potential than the tetraploid entry. This greater soil water extraction did not result in greater dry matter production for the diploid compared with the tetraploid entry, which suggests a less efficient use of water by the diploid.

The entry × water treatment interaction for LWP was significant because differences in LWP were greater between the tetraploid and the diploid entry in the 50 than 150% water treatment (Table 1). Values of LWP were 0.6 and 0.3 MPa less negative for the tetraploid than diploid entry at the 50 and 150% water treatment, respectively, suggesting that the tetraploid entry maintained better plant water relations than the diploid entry. This difference coincides with the differences in soil water potential at the 50% water treatment (Fig. 2) and probably contributed to the significantly greater dry matter production for the tetraploid compared with the diploid entry at the 50% water treatment (Fig. 1).

The entry × N × water × Haun stage interaction was significant for CER at both the 50% (Fig. 3) and 150% water treatment (Fig. 4). The interaction for plants at the 50% water treatment was mainly due to difference in CER between the N treatments with increasing Haun stage for both entries. Values for CER of the tetraploid entry at the 50% water treatment were significantly greater than the diploid entry at the final three Haun stages for the 10 kg N ha<sup>-1</sup>, and at the final two Haun stages for the 134 kg N ha<sup>-1</sup> treatment (Fig. 3). Values of CER at 50% water treatment were significantly greater for the tetraploid (14.2 μmol m<sup>-2</sup> s<sup>-1</sup>) compared with the diploid (12.4 μmol m<sup>-2</sup> s<sup>-1</sup>) entry when averaged across all Haun stages. These results differ from those in the 150% water treatment where CER did not differ among treatments for either the diploid (14.8 μmol m<sup>-2</sup> s<sup>-1</sup>) or tetraploid (14.9 μmol m<sup>-2</sup> s<sup>-1</sup>) entries (Fig. 4). Except for the second Haun

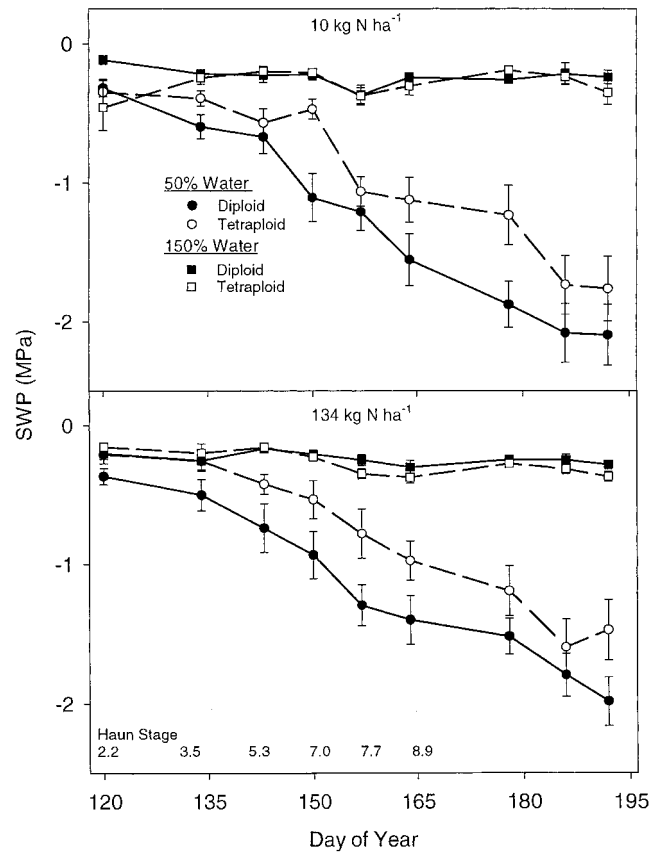


Fig. 2. Soil water potential (SWP) determined with thermocouple psychrometers at 45-cm depth for diploid and tetraploid entries of Russian wildrye at 50 and 150% of average rainfall and at 10 and 134 kg N ha<sup>-1</sup>. Data are means for 1994, 1995, and 1996. The Haun stage is presented above the x-axis. Final forage yields were determined at Haun Stage 9. Vertical bars are standard errors of the mean.

stage (Haun Stage 6) for the tetraploid entry at the 50% water treatment, N rate had no effect on CER within entries and water treatments. Averaged across Haun stages the tetraploid entry was able to maintain higher CER than the diploid entry at the more stressful 50% water treatment. The decrease in CER for both the 50 and 150% water treatments as Haun stage increased was probably due to leaf age effects (Dantuma, 1973) and temperature and leaf water stress reducing stomatal conductance.

The trends in T for both the diploid and tetraploid entries were similar to CER responses for the 50% (Fig. 3) and 150% (Fig. 4) water treatments. The entry ×

Table 1. Leaf water potential for diploid and tetraploid entries of Russian wildrye grown at 50 and 150% of average rainfall. Data are means across 1994, 1995, and 1996.

Entry	Water level	Leaf water potential MPa
	% of average	
Diploid	50	A† -2.0a‡
Tetraploid	50	A -1.4b
Diploid	150	B -1.6a
Tetraploid	150	A -1.3b

† Water levels within an entry means with different upper case letters are different at 0.05 level of probability.

‡ Entries at the same water level with different lower case letters are different at 0.05 level of probability.

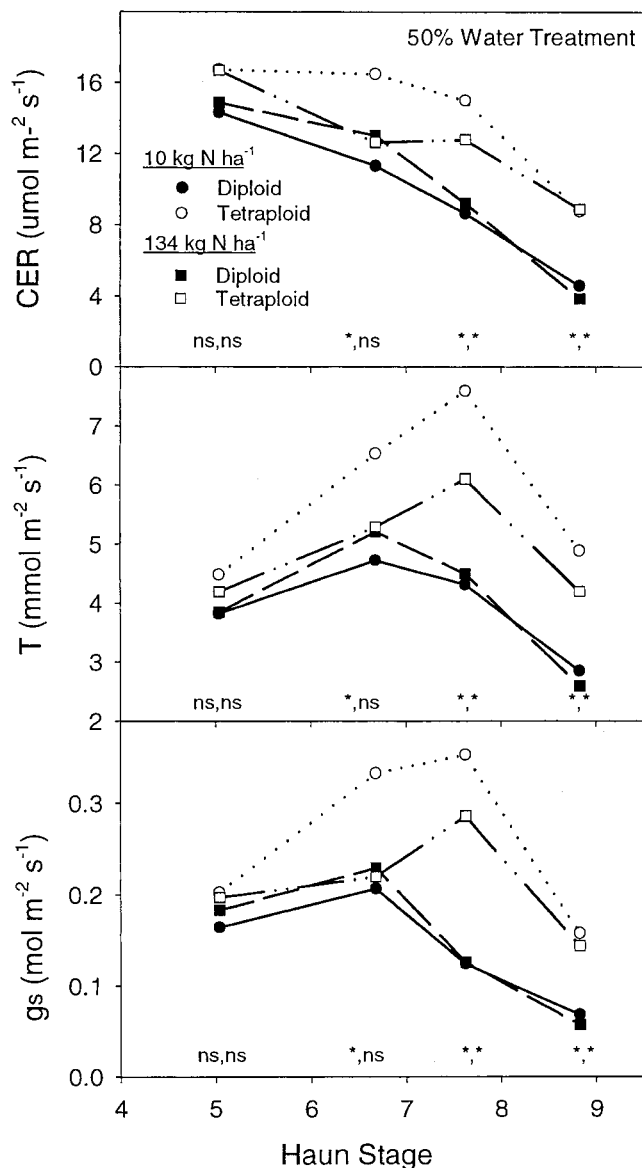


Fig. 3. Carbon exchange rate (CER) transpiration (T), and stomatal conductance (gs) for diploid and tetraploid entries of Russian wildrye grown at 10 and 134  $\text{kg N ha}^{-1}$  and 50% of average rainfall. Data are means for 1994, 1995, and 1996. Significance at 0.05 level of probability between entries at the same N rate is indicated with an \* or ns (not significant) at each Haun stage for the 10 and 134  $\text{kg N ha}^{-1}$  comparisons, respectively.

$\text{N} \times \text{water} \times \text{Haun stage}$  interaction was significant mainly due to changes in rate of T with advancing Haun stage. The trend at the 50% water treatment was for greater T in the tetraploid compared with the diploid entry. For the tetraploid entry, rates of T were generally greater at the 10 than 134  $\text{kg N ha}^{-1}$  treatments, whereas for the diploid entry T was not affected by N rate. In the 150% water treatment, there were no consistent differences in T between the diploid and tetraploid entries or among N rates. Overall, T differed significantly between entries, averaging 5.2 and 6.0  $\text{mmol m}^{-2} \text{s}^{-1}$  for the diploid and tetraploid entries, respectively.

The entry  $\times \text{N} \times \text{water} \times \text{Haun stage}$  interaction was significant for gs, and the changes in gs across Haun

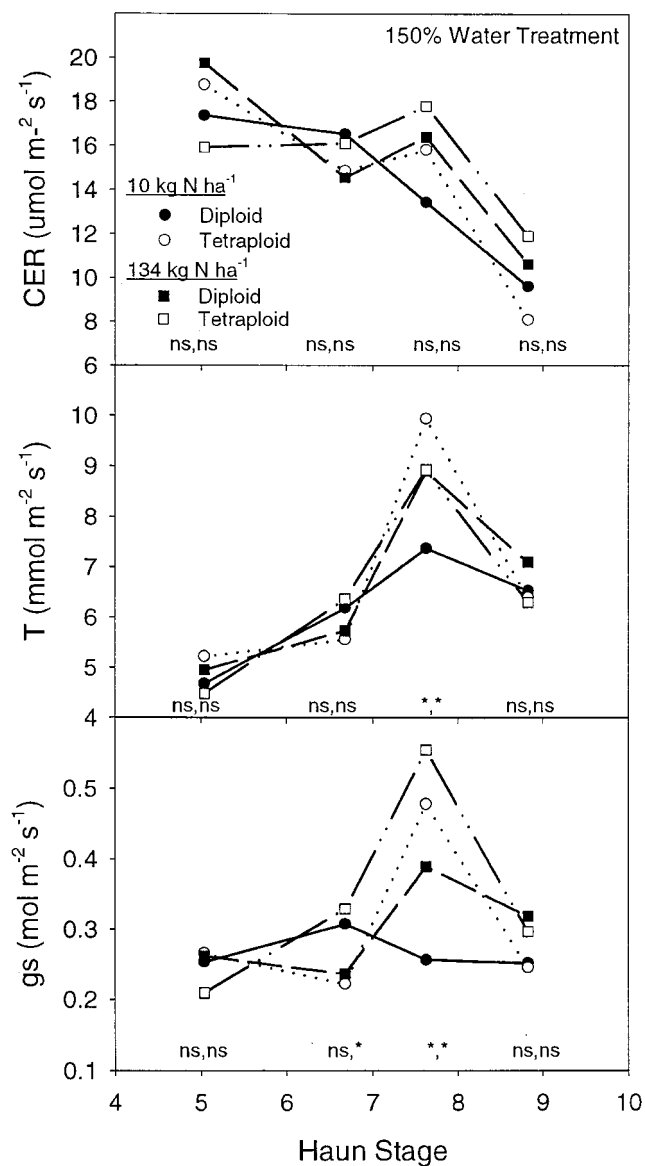


Fig. 4. Carbon exchange rate (CER), transpiration (T), and stomatal conductance (gs) for diploid and tetraploid entries of Russian wildrye grown at 10 and 134  $\text{kg N ha}^{-1}$  and 150% of average rainfall. Data are means for 1994, 1995, and 1996. Significance at the 0.05 level of probability between entries at the same N rate is indicated with an \* or ns (not significant) at each Haun stage for the 10 and 134  $\text{kg N ha}^{-1}$  comparisons, respectively.

stages closely followed the pattern for T for both the 50% (Fig. 3) and 150% (Fig. 4) water treatments. The tetraploid entry at 50% water and 10  $\text{kg N ha}^{-1}$  had significantly greater gs than the diploid entry at all but the first Haun stage. At the 50% water and 134  $\text{kg N ha}^{-1}$ , the tetraploid entry had greater gs than the diploid entry at the final two Haun stages. Similar to the CER and T rates, N did not affect gs for the diploid entry. For the 150% water treatment, differences in gs between the tetraploid and diploid entries were significant at the third Haun stage for 10  $\text{kg N ha}^{-1}$  and at the second and third Haun stage for 134  $\text{kg N ha}^{-1}$  rate (Fig. 4). Overall, gs differed significantly between entries, averaging 0.21 and 0.28  $\text{mol m}^{-2} \text{s}^{-1}$  for the diploid and

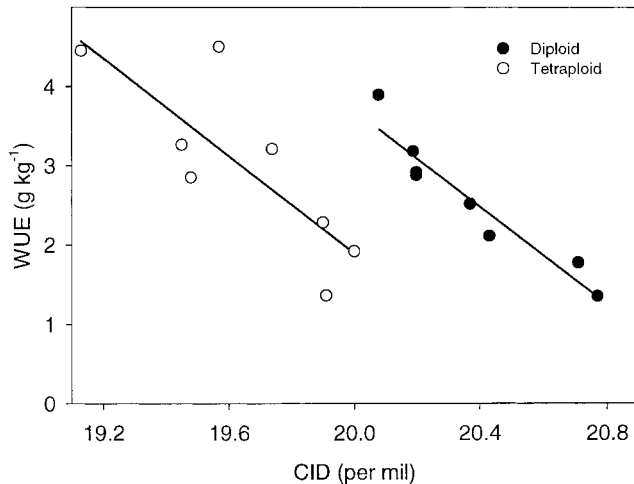


Fig. 5. Relationship between carbon isotope discrimination (CID) in leaves and field measured water use efficiency (WUE) for diploid and tetraploid entries of Russian wildrye in 1994 and 1995. Regression equations are  $WUE = 65.01 - 3.06(CID)$ , ( $r^2 = 0.91$ ) and  $WUE = 63.40 - 3.07(CID)$ , ( $r^2 = 0.65$ ) for diploid and tetraploid entries, respectively.

tetraploid entries, respectively.

Leaf CID values differed significantly between entries, water levels, and N rates; however, the difference in CID between entries was consistent across water levels and N rates. The diploid entry had a significantly greater CID, averaging 20.37‰ compared with 19.65‰ for the tetraploid entry. Carbon isotope discrimination was significantly less at the 50% than 150% water treatment, averaging 19.81‰ and 20.21‰, respectively. In contrast to reductions in LWP created by the 50% water treatment that resulted in a lower CID, reductions in plant N status created by the lower N rate of 10 kg N ha<sup>-1</sup> resulted in a greater CID of 20.13‰ compared with 19.90‰ for plants grown at the 134 kg N ha<sup>-1</sup>. Carbon isotope discrimination was not statistically different in 1994 (19.96‰) than 1995 (20.06‰). A nonsignificant entry × year interaction indicated that differences in CID between entries were consistent across years. Frank and Berdahl (1999) previously reported that WUE was greater for tetraploid compared with diploid Russian wildrye, especially at greater soil water deficits. In the present study, the slope of the regression of WUE on CID was negative for both the diploid and tetraploid entries (Fig. 5). Values of  $r^2$  were 0.91 and 0.65 for the diploid and tetraploid entries, respectively, which suggests CID may be a reliable indicator of changes in WUE in Russian wildrye. Simple correlation coefficients between CID and instantaneous WUE determined from gas exchange measurements of CER/T, CER/gs, and atmospheric carbon dioxide concentration/leaf intercellular carbon dioxide concentration (Ci/Ca) for the combined diploid and tetraploid entries were near zero in contrast to a significant  $r$  of  $-0.66^{**}$  for CID and field measured WUE (Table 2). Johnson et al. (1990) reported WUE, determined on the basis of dry matter production, was significantly correlated with CID in crested wheatgrass and Altai wildrye.

The entry × water × Haun stage interaction for dry

Table 2. Simple correlations ( $r$ ) for WUE, CID, CER/T, CER/gs, and Ci/Ca combined across diploid and tetraploid entries of Russian wildrye.

Trait	Trait			
	CID	CER/T	CER/gs	Ci/Ca
WUE	$-0.66^{**}$	$0.48^*$	$0.49^*$	$-0.53^*$
CID		$-0.12$	$0.03$	$-0.03$

\*, \*\* Indicates statistical significance at the 0.05 and 0.01 probability levels, respectively ( $n = 16$ ).

matter production was due to the tetraploid entry producing more dry matter than the diploid at the 50%, but not the 150% water treatment (Fig. 1). This greater dry matter production in the tetraploid compared with the diploid entry under the drought condition created by the 50% water treatment suggests the tetraploid entry should provide for greater sustained production in the Northern Great Plains where annual precipitation averages less than 400 mm. The mechanisms that enable the tetraploid entry to produce more forage under drought are probably complex and not easily determined. However, the CER, T, gs, and LWP measurements at the 50% water treatment do provide evidence that the plant water relationships of the tetraploid entry should enhance dry matter production and perhaps drought tolerance.

Values of LWP in the 50% water treatment averaged 0.6 MPa less negative for the tetraploid than the diploid entry, which probably resulted in greater tissue turgor and growth. Asay et al. (1996) reported that tetraploid entries of Russian wildrye had greater water content than diploid entries. Gas exchange parameters of CER, T, and gs were all greater for the tetraploid at the 50% water treatment (Fig. 3), suggesting more efficient utilization of the limited water available for processes that contribute to dry matter production. In the 150% water treatment, however, the tetraploid entry did not produce more dry matter than the diploid entry, which further suggests that the total plant water requirement for dry matter production of the tetraploid entry is probably similar to that of the diploid entry. Although the weekly applications of water were the same for both entries, the watering regime may have favored the tetraploid entry compared with the diploid entry, because of apparent water conserving traits in the tetraploid entry, which resulted in greater plant tissue turgor and, thus, CER and gs.

The difference in CID between the tetraploid (19.65‰) and the diploid (20.37‰) entries was 0.72‰, which is similar to the difference in CID values reported by Asay et al. (1996) between natural tetraploid accessions (17.2‰) of Russian wildrye and the cultivar Vinall (18.1‰). The negative relationship between CID and WUE, also, was similar to that reported by Johnson et al. (1990) for crested wheatgrass and Altai wildrye and Read et al. (1993) for crested wheatgrass. On the basis of these reported relationships, the tetraploid Russian wildrye entry utilizes water more efficiently than the diploid entry for dry matter production.

Carbon isotope discrimination is considered a season-long integrator of plant response to environmental

stresses (Johnson et al., 1990) and is genetically controlled (Ehleringer et al., 1990; Asay et al., 1996). The greater water stress, indicated by lower LWP (Table 1) at the 50% water treatment for the diploid compared with the tetraploid entry, was associated with a lower  $g_s$  for the diploid entry (Fig. 3). A lower  $g_s$  reduces CER and CID through stomatal closure (Cowan, 1982; Farquhar et al., 1982) which is associated with the lower CID of 19.81‰ compared with 20.21‰ in the 50 and 150% water treatments, respectively. However, CID for the tetraploid entry (19.65‰) was lower than that for the diploid entry (20.37‰). This pattern plus a greater CER and  $g_s$  (Fig. 3), and LWP (Table 1) at the 50% water treatment strongly suggests the tetraploid entry has mechanisms that conserve water and produce more dry matter than the diploid entry.

Combined across entries the instantaneous gas exchange measurements for WUE made on individual leaves were poorly correlated to field-measured WUE (Table 2), which may reflect either a loose coupling between these traits or the temporal disconnect between the short-term leaf measurements and long-term WUE measurements made in the field plots. Instantaneous measurements of WUE are strongly tied to  $C_i/C_a$  which is mainly a function of stomatal conductance and chloroplast demand for carbon dioxide. In contrast, WUE determined from dry matter production and soil water loss is an integration of the season's environment on plant water relations and dry matter production. Although our measurements showed field-measured WUE was significantly correlated with CER/T, CER/ $g_s$  and  $C_i/C_a$ , correlation coefficients were only 0.48,\* 0.49,\* and -0.53,\* respectively. Read et al. (1993) reported a close association between several gas exchange parameters and instantaneous WUE in crested wheatgrass.

These results provide information on rates of physiological processes and water relationships in diploid (Vinnall) and tetraploid (a composite of six populations) Russian wildrye. The tetraploid compared with the diploid entry of Russian wildrye used water more efficiently under the water limiting conditions common to the Northern Great Plains. This is a desirable characteristic in the water limiting areas where Russian wildrye is best adapted. In summary, increased seedling vigor shown by the tetraploid compared with the diploid populations in previous studies and the favorable plant water relations shown in this present study further underscores the potential that tetraploid populations of Russian wildrye have in water deficit environments. However, since the diploid Russian wildrye was represented by a single cultivar these results should not be extended to all diploid cultivars.

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